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ON THE DISTRIBUTION OF ABNORMALITIES IN THE INFLORESCENCE OF SPIRAEA VANHOUTTEI

J. Arthur Harris

I. Introductory Remarks

Experimental breeders, primarily de Vries, have shown that in certain races individuals of more or less mutually exclusive characteristics may regularly occur in fairly constant proportions. Students of hybridization have devoted their chief effort for the past fifteen years to a study of the laws of segregation of parental characters in filial generations. Those interested in experimental morphology recognize the fact that a pure bred individual may in the course of its ontogeny display characteristics which might belong to distinct varieties or species.

In its relation to both genetic and morphogenetic problems the investigation of the distribution of abnormalities among the synchronously developed organs of the same individual seems of importance.

The purpose of the present note is to call attention to peculiarities of the frequency disrtibutions of certain abnormalities of the pedicels in one of the most splendid garden spiraeas, *S. Vanhouttei.*

II. History of Spiraea Vanhouttei and Discussion of Morphology of Inflorescence

1. *History of S. Vanhouttei* (Briot) Zbl.

Briot writes of the origin of the form which he refers to as *Spiraea aquilegifolia vanhouttei:*[1] "Cette variété, obtenue par M. Billard . . . de graines du *Spiraea aquilegifolia.*" He also states: "Le *Spiraea aquilegifolia* est, dit-on, une forme du *Spiraea trilobata.*" In his original description Zabel[2] gives no statement as to where or when this "hybrid" was formed. In a later paper[3] he merely refers to it as a hybrid between *Spiraea cantoniensis* and *S. trilobata*, without giving any details or actual proof of its hybrid origin.

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[1] Briot, Rev. Hort. **37**: 269. 1866.

[2] Zabel, H., Gart. Zeit. **3**: 496. 1884.

[3] Zabel, H., Mitteil. Deutsch. Dend. Ges. **1904**: 59.

Schneider[4] follows Zabel in regarding the form as a hybrid between *S. cantoniensis* and *S. trilobata*. So far as I can make out there is no really valid ground for this conclusion.

The early writers on *S. vanhouttei* noted abnormalities of the inflorescence. Briot[5] describes some in the original material. Zabel[6] has even described a new form, which he calls *S. Vanhouttei* var. *phyllothyrsa*, in part distinguished by abnormalities of the inflorescence.

Those who desire to compare the anomalies described in this paper with those hitherto recorded may consult these papers. My purpose has not been to describe in detail all the types of aberration which may occur, but rather to throw them into categories usable for statistical analysis.

2. *Descriptive Morphology of Inflorescence*

The normal inflorescence of *S. Vanhouttei* is a many-flowered umbel-like raceme. In general, the pedicels originate fairly close together, but occasionally the lowermost flowers are considerably scattered.

Normally each ray, as I shall sometimes call the pedicels, is simple, terminated by a single flower, but occasionally more or less compounded. The normal inflorescence, composed exclusively of simple rays, is too familiar to require illustration. Figs. 17 and 18 give a good idea of the abnormal inflorescence, the latter figure representing a rather advanced though by no means extreme stage of compounding.

In general it is the lowermost rays of the flower cluster which become compound, but there are inflorescences, and perhaps individual plants, in which this is not true.

The range of variation in the abnormal pedicels is, as shown in Figs. 1–16,[7] of the two plates, very great. In the earlier work with the form I devoted much attention to the attempt to classify the various anomalies into logical groups: for example, to distinguish between synanthies and the compounding of the flower stalk, and between synanthies and the production of an accessory pedicel immediately below the terminal receptacle.

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[4] Schneider, C. K., Illust. Hand. Laubholzk. 465. 1905.

[5] Briot, Rev. Hort. **37**: 269. 1866.

[6] Zabel, H., Mitteil. Deutsch. Dend. Ges. **1904**; 59–60.

[7] Figs. 1–16 are natural size, Figs. 17–18 twice natural size.

Typical cases of synanthy are shown from the side in Figs. 5, 6, 8 and 9 and from below in Figs. 2 and 3, to which Fig. 1 of a normal flower is joined for comparison. Examples of the production of an accessory pedicel below the normal receptacle are shown from the side in Fig. 10 and from below in Fig. 4. But all possible gradations may be found between these two types of anomalies: hence it is idle to recount the criteria which have been applied in an attempt to distinguish between them. For example, it is difficult to decide just how the cases illustrated in Figs. 7, 11, 12 and 14 shall be classified. They combine in some degree the characteristics of perfectly constituted secondary inflorescences, of synanthous flowers and those in which there is a production of an adventitious pedicel from below the receptacle.

The numbers of flowers involved in synanthy varies considerably. Generally it is 2, but 3, 4 or 5 may be found. Figs. 2–3, 5–11, and 14 serve as illustrations. The number of secondary rays originating below the inflorescence is also variable. It is interesting to note that very frequently, and I believe in the great majority of the cases, the secondary pedicel extends considerably above the flower below which it originates, as shown in Figs. 10 and 12.

Between synanthy, or pedicels showing secondary rays inserted below the receptacle, to the most perfectly formed secondary "umbels," as shown in Fig. 16, all possible transitions, both in number of flowers and perfection of formation, are found.

Ordinarily the rays of the secondary umbels are inserted at about the same position, but occasionally examples are found in which one ray is considerably lower than the rest, or in which the lowermost rays are rather scattered. The number of secondary pedicels varies greatly.

Some abnormalities of inflorescence structures are almost invariably formed in any large series of plants. Without going into details concerning the general observations of the past several years, I think it may be safely stated that variation in the inflorescence is to some extent dependent upon the peculiarities of the individual plants and to some extent determined by environmental conditions.

III. Discussion and Analysis of Data

The first problem to require consideration is that of the frequency and the nature of the distribution of abnormal pedicels.

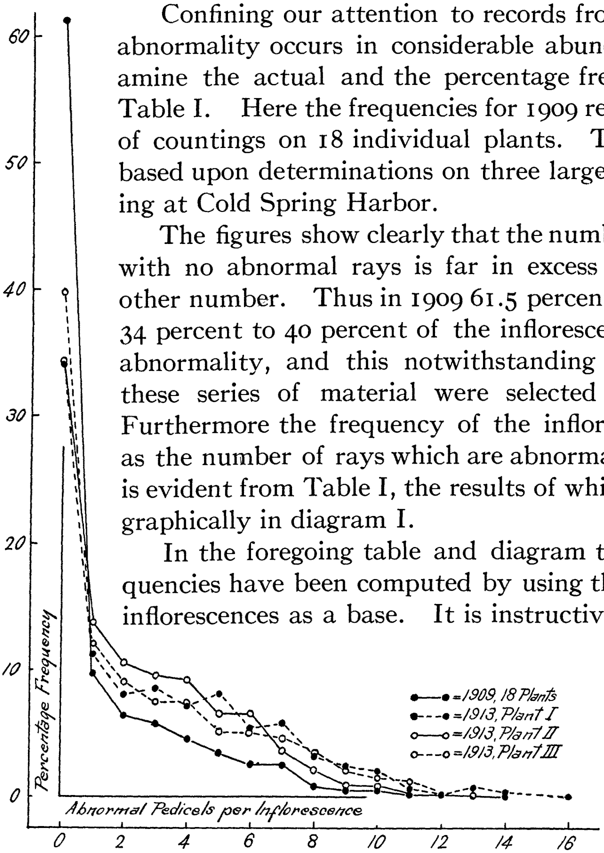

DIAGRAM 1. Percentage frequencies of number of abnormal pedicels per inflorescence in all inflorescences.

Confining our attention to records from plants in which abnormality occurs in considerable abundance, we may examine the actual and the percentage frequencies given in Table I. Here the frequencies for 1909 represent the results of countings on 18 individual plants. Those for 1913 are based upon determinations on three large individuals growing at Cold Spring Harbor.

The figures show clearly that the number of inflorescence with no abnormal rays is far in excess of these with any other number. Thus in 1909 61.5 percent and in 1913 from 34 percent to 40 percent of the inflorescences were without abnormality, and this notwithstanding the fact that all these series of material were selected for abnormality. Furthermore the frequency of the inflorescences decreases as the number of rays which are abnormal increases. This is evident from Table I, the results of which are represented graphically in diagram I.

In the foregoing table and diagram the percentage frequencies have been computed by using the total number of inflorescences as a base. It is instructive to determine the relative frequencies of different number of abnormalities in the inflorescences which have at least one abnormal pedicel. The results are shown in Table II, and represented graphically in diagram 2.

Both methods give skew distribution, the highest frequency falling on 0 or 1 abnormal ray, and the frequency decreasing from this class to those with higher numbers of abnormal pedicels.

That the skewness of distribution of the number of abnormal pedicels per inflorescence is not due to skewness in the distribution of number of pedicels in the inflorescence as a whole is shown clearly by diagram 4, which gives the percentage frequencies of number of pedicels in three of the series. All of these distributions are fairly symmetrical.

TABLE I

Actual Frequencies, f, and Percentage Frequencies of Number of Abnormal Pedicels per Inflorescence in All the Inflorescences

Number of Abnormal Pedicels	1909, 18 Plants		1913, Plant I		1913, Plant II		1913, Plant III	
	f	%	*f*	%	*f*	%	*f*	%
0	1,255	61.51	388	34.18	334	34.25	364	39.91
1	203	9.95	130	11.45	136	13.95	111	12.17
2	132	6.47	93	8.19	105	10.77	82	8.99
3	120	5.88	98	8.63	94	9.64	68	7.46
4	95	4.66	83	7.31	89	9.13	66	7.24
5	71	3.48	95	8.37	65	6.67	46	5.04
6	55	2.69	64	5.63	65	6.67	48	5.26
7	54	2.65	68	5.99	37	3.79	42	4.61
8	19	.93	38	3.35	22	2.26	30	3.29
9	11	.53	29	2.56	10	1.02	21	2.30
10	12	.59	23	2.03	8	.82	16	1.75
11	7	.34	9	.79	3	.31	13	1.43
12	5	.24	3	.26	3	.31	3	.33
13	—	—	9	.79	2	.21	1	.11
14	1	.04	4	.35	2	.21	1	.11
15	—	—	—	—	—	—	—	—
16	—	—	1	.08	—	—	—	—
Total......	2,040	99.96	1,135	99.96	975	100.01	912	100.00

TABLE II

Percentage Frequencies of Number of Abnormal Pedicels in Abnormal Inflorescences Only

Number of Abnormal Pedicels	Percentage Frequency			
	1909, 18 Plants	1913, Plant I	1913, Plant II	1913, Plant III
1	25.86	17.40	21.22	20.26
2	16.82	12.44	16.38	14.96
3	15.28	13.12	14.66	12.41
4	12.10	11.11	13.88	12.04
5	9.04	12.72	10.14	8.40
6	7.01	8.56	10.14	8.76
7	6.87	9.10	5.77	7.66
8	2.42	5.08	3.43	5.47
9	1.40	3.88	1.56	3.83
10	1.52	3.08	1.25	2.92
11	.89	1.20	.47	2.37
12	.63	.40	.47	.55
13	—	1.20	.31	.18
14	.12	.54	.31	.18
15	—	—	—	—
16	—	.13	—	—

The fact that the three collections made from large individuals in the spring of 1913 show the same type of frequency distribution as

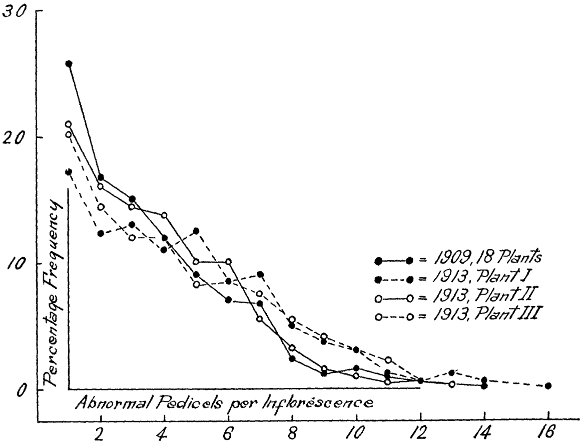

DIAGRAM 2. Percentage frequencies of number of abnormal pedicels per inflorescence in abnormal inflorescences.

TABLE III

Number of Abnormal Pedicels per Inflorescence in Inflorescences of Various Total Numbers of Pedicels

Total Pedicels in Inflorescence	Abnormal Pedicels													Total
	1	2	3	4	5	6	7	8	9	10	11	12	14	
3– 5...	—	—	1	—	—	—	—	—	—	—	—	—	—	1
6– 8...	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9–11...	1	1	—	—	—	—	—	—	—	—	—	—	—	2
12–14...	11	3	—	—	—	—	1	—	—	—	—	—	—	15
15–17...	23	13	12	8	10	2	3	—	—	—	—	—	—	71
18–20...	54	43	33	31	16	11	12	—	1	3	1	1	—	206
21–23...	70	38	37	31	24	17	19	8	5	3	4	2	—	258
24–26...	27	20	23	18	12	19	16	9	5	4	2	1	1	157
27–29...	14	7	9	4	7	5	3	2	—	2	—	1	—	54
30–32...	3	5	4	3	2	1	—	—	—	—	—	—	—	18
33–35...	—	2	—	—	—	—	—	—	—	—	—	—	—	2
36–38...	—	—	1	—	—	—	—	—	—	—	—	—	—	1
Total..	203	132	120	95	71	55	54	19	11	12	7	5	1	785

the massed materials of 1909 is sufficient proof that the skew distribution of number of abnormal rays per inflorescence is not due to any process of combination of materials from individuals differentiated with respect of the number of abnormal rays which they produce.

Table III shows the distribution of number of abnormal rays per inflorescence in groups of inflorescences of similar numbers of total rays in the data for 1909. In this table are included wholly normal inflorescences, all of which are entered in the zero class, as well as the inflorescences which contain abnormalities. Whenever the countings are sufficiently numerous to justify conclusions, the frequency distri-

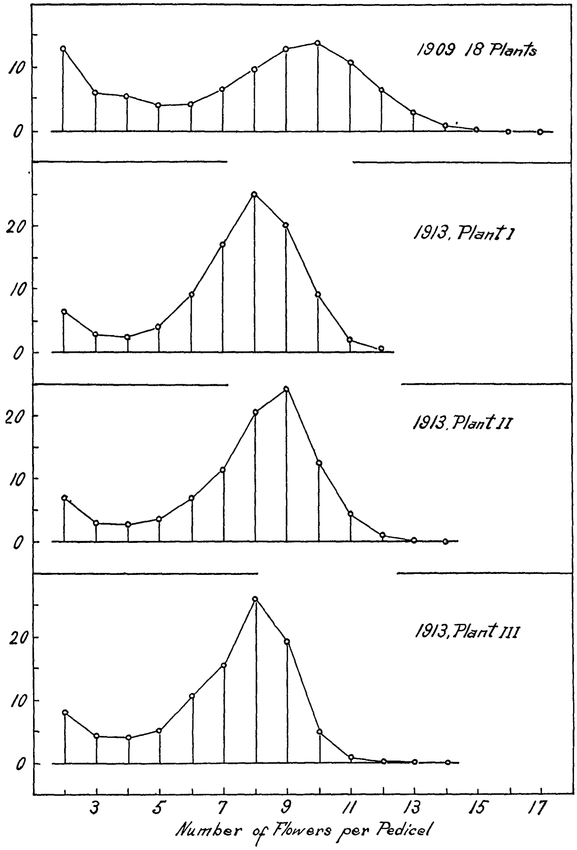

DIAGRAM 3. Percentage frequencies of number of abnormal flowers per pedicel in abnormal pedicels. Note the bimodal nature of the distribution.

bution of numbers of abnormal pedicels per inflorescence in groups of inflorescence with similar number of pedicels is skew, just as it is in the series as a whole.

The second peculiarity of the distribution of abnormality in the inflorescences of this species is to be seen in the frequency of numbers of flowers per pedicel. This is excellently shown for a combined series of countings made from 18 shrubs in 1909 and from three large individual plants examined in 1913. These frequencies, reduced to a percentage basis, are represented graphically in diagram 3.[8]

TABLE IV

Bimodal Distribution of Number of Flowers per Pedicel in the Abnormal Inflorescences of Individual Plants

Plant Number	Number of Flowers Produced by Abnormal Pedicels																Total
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1	27	5	7	9	11	15	31	31	59	40	17	8	1	–	–	–	261
2	1	3	–	2	1	3	5	3	2	–	–	–	–	–	–	–	20
3	11	6	9	6	8	19	8	2	–	–	–	–	–	–	–	–	69
4	26	15	11	6	8	6	6	16	9	6	2	–	–	–	–	–	111
5	8	4	8	5	4	10	12	24	13	7	3	–	–	–	–	–	98
6	22	7	10	4	6	12	10	16	19	12	6	1	–	–	–	–	125
7	12	9	7	10	12	7	15	13	8	3	–	–	–	–	–	–	96
8	31	25	15	11	7	14	12	31	36	53	62	55	27	9	1	–	389
9	20	6	14	7	9	10	8	15	10	8	3	–	–	–	–	–	110
10	8	3	2	1	1	4	6	6	4	–	–	–	–	–	–	–	35
11	21	11	5	5	3	4	21	22	15	9	3	–	–	–	–	–	119
12	3	3	3	–	4	13	8	3	–	–	–	–	–	–	–	–	37
13	41	31	16	14	16	13	31	50	47	28	21	4	1	–	–	–	313
14	19	10	9	7	3	8	10	12	18	26	11	3	–	–	–	–	136
15	34	10	7	10	9	9	22	35	42	41	26	6	2	–	–	–	253
16	23	12	11	9	8	25	32	33	21	7	4	–	–	–	–	–	185
17	22	7	6	6	6	8	11	14	15	6	6	3	1	–	–	–	111
18	35	6	9	9	8	8	26	47	81	61	28	5	–	–	–	1	324
Total. .	364	173	149	121	124	188	274	373	399	307	192	85	32	9	1	1	2,792

In all four series there is a major mode on 8, 9 or 10 flowers per pedicel and a secondary mode on two flowers per pedicel.

This species adds, therefore, one other to the series of dimorphic characters, which have been reviewed elsewhere.[9]

That the bimodal condition for the 1909 series is not due to the mixing of inflorescence from a series of shrubs, some of which have a modal frequency of two flowers per pedicel in the abnormal pedicels and other shrubs which have a modal frequency on a higher number of flowers in the secondary umbels, as we may for convenience call them, is shown at once by an examination of the frequency distributions for number of flowers per pedicel in the abnormal pedicels of the individual shrubs. This is given in Table IV. From these data it appears that 16 of the 18 individual plants which contributed to the total series of 2,792 abnormal rays upon which the polygon for 1909 in diagram 4 is based, show a distinct secondary mode on 2 flowers per pedicel.

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[8] A few synanthous flowers have been included among the two-flowered pedicels.

[9] Harris, J. Arthur, A Bimodal Variation Polygon in *Syndesmon thalectroides* and its Morphological Significance, Amer. Nat. 44: 19–30. 1910.

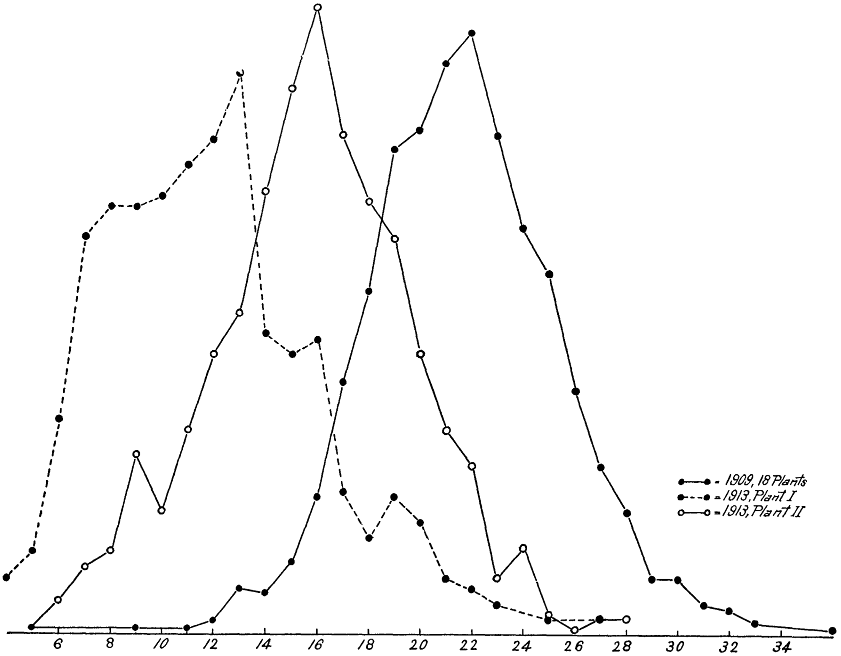

DIAGRAM 4. Frequencies of number of pedicels in *Spiraea.*

The two plants which are exceptions to this rule are represented by only 20 and 37 pedicels each. These numbers are entirely too small to justify any conclusion concerning the nature of the distributions. Had larger series of countings from these individuals been available, they might have shown the same bimodal condition as the other sixteen.

The whole series of available data may be taken to indicate with remarkable consistency that the bimodal nature of the distribution of number of flowers per pedicel is not due to heterogeneity of material, so far as this may originate from the combination of inflorescences derived from differentiated individuals. It represents, therefore, the resultant of some group of factors innate in the individual.

Having eliminated the possibility of an influence of the individual plant as a determining factor of the peculiar frequency distribution, it seems worth while to enquire whether any characteristic of the inflorescence itself may have an influence upon the distribution of the number of flowers per pedicel. It is quite conceivable, for example, that the inflorescences which are the most highly abnormal as measured by the total number of abnormal pedicels, should have a larger number of flowers in their secondary umbels than those which are only very slightly abnormal. The combination of a series of inflorescences, some only slightly abnormal and others highly abnormal, might, under such conditions, result in a bimodal distribution of flower number in the series of pedicels from the combined inflorescences.

TABLE V

Bimodal Distribution of Number of Flowers per Pedicel in Inflorescences with Various Numbers of Abnormal Flowers per Pedicel

Total Abnormal Pedicels	Number of Flowers Produced by Abnormal Pedicels											Total
	2	3	4	5	6	7	8	9	10	11	12	
1	30	8	5	8	12	18	28	12	6	3	–	130
2	17	13	9	8	19	33	31	35	17	4	–	186
3	27	13	13	12	32	52	63	50	28	4	–	294
4	21	7	20	18	42	58	62	62	33	9	–	332
5	34	15	13	19	40	66	131	103	41	12	1	475
6	24	16	4	15	31	56	89	91	47	10	1	384
7	26	6	9	23	49	79	132	96	44	12	–	476
8	15	4	4	11	20	50	80	64	42	13	1	304
9	16	7	7	7	29	54	59	59	20	3	–	261
10	8	2	1	11	20	54	67	46	16	5	–	230
11	2	3	1	2	12	16	29	28	6	–	–	99
12	1	–	1	3	1	4	13	10	2	1	–	36
13	2	–	–	–	7	20	42	26	18	2	–	117
14	2	–	–	1	4	15	20	12	1	1	–	56
16	–	–	–	1	1	5	5	4	–	–	–	16
Total......	225	94	87	139	319	580	851	698	321	79	3	3,396

Table V shows the number of flowers per pedicel in the 3,396 abnormal pedicels produced by the 747 inflorescences examined from

Plant I in 1913, arranged according to the number of abnormal pedicels per inflorescence. This table is quite typical of the others which have been made. The bimodal distribution characterizes all the arrays in which the number of observations is large enough to give the distributions critical value.

Differentiation between individual plants and differentiation due to correlation between the characteristics of the pedicels and those of the inflorescence would seem to be the most probable source of a spurious bimodality in the frequency distributions of number of flowers per pedicel. That neither of these factors underlies the observed form of the frequency distribution seems quite clear from the foregoing tables. Bimodiality seems rather to be due to innate factors operative in the morphogenesis of the individual pedicels.

Now in examining the graphs on diagram 3 the reader will note that the mode on 2 flowers per pedicel is but a transition stage to the higher mode—not represented in the diagram—on a single flower per pedicel—that is to the normal condition.

TABLE VI

Distribution of Number of Flowers per Pedicel for All Pedicels

Number of Flowers per Pedicel	Series			
	1909, 18 Shrubs	1913, Plant I	1913, Plant II	1913, Plant III
1	14,250	8,436	5,196	5,714
2	364	225	177	193
3	173	94	83	103
4	149	87	72	101
5	121	139	87	119
6	124	319	159	245
7	188	580	280	367
8	274	851	506	616
9	373	698	601	458
10	399	321	305	114
11	307	79	112	22
12	192	3	35	8
13	85	—	9	3
14	32	—	1	1
15	9	—	—	—
16	1	—	—	—
17	1	—	—	—
Total........	17,042	11,832	7,623	8,064

Tabulating the actual number of flowers per pedicel for all pedicels examined, the frequencies in Table VI are obtained.

These seriations bring out clearly that there are minimum frequencies on four flowers per pedicel, and that the number of pedicels increases rapidly as the number of flowers becomes smaller, reaching a maximum on the single flowered (normal) pedicel, and that on the other hand it increases more gradually as the number of flowers becomes larger to a secondary maximum on 8–10 flowers per pedicel.

Concluding Remarks

This paper provides illustrations of the chief types of variation which occur in the inflorescence of *Spiraea Vanhouttei*, and records the results of statistical studies of the distribution of these abnormalities.

The inflorescence of *S. Vanhouttei* is described by taxonomists as a simple raceme-like umbel. A number of the pedicels are, however, often compound. The compounding may range from a simple synanthous condition to the production of a perfect, many-flowered, secondary umbel in the place of the solitary flower which normally terminates the pedicel.

The distribution of abnormal pedicels among the inflorescences in plants in which abnormality is of frequent occurrence is not to be represented by a normal or Quetelet's curve but forms a one-sided or skew frequency distribution, in which the frequency of occurrence decreases as the number of abnormal pedicels per inflorescence becomes larger. This is the first law of variation in the abnormalities of the inflorescence.

If the normal pedicels be included with the abnormal to form a single frequency distribution of number of flowers per pedicel in inflorescences in which some of the pedicels are abnormal, it will be seen that the two flowered pedicels form a transition frequency from classes of larger numbers of flowers to those with a single flower per inflorescence.

On examining these bimodal frequency distributions the reader may be tempted to formulate some hypotheses concerning the coexistence of determiners of mutually exclusive characters or concerning the segregation of alternative, but variable, characters in the morphogenetic processes of the individual plants. *S. Vanhouttei* is known to be of garden origin and is supposedly a hybrid between *S. cantoniensis* and *S. trilobata*. The evidences are not, however, such as would be readily accepted by a careful geneticist. Furthermore, both of these assumed parent species have simple inflorescences.

S. Vanhouttei is horticulturally such a splendid form that it would be well worth while for some unoccupied geneticist to attempt further crosses in this group of Spiraeas.

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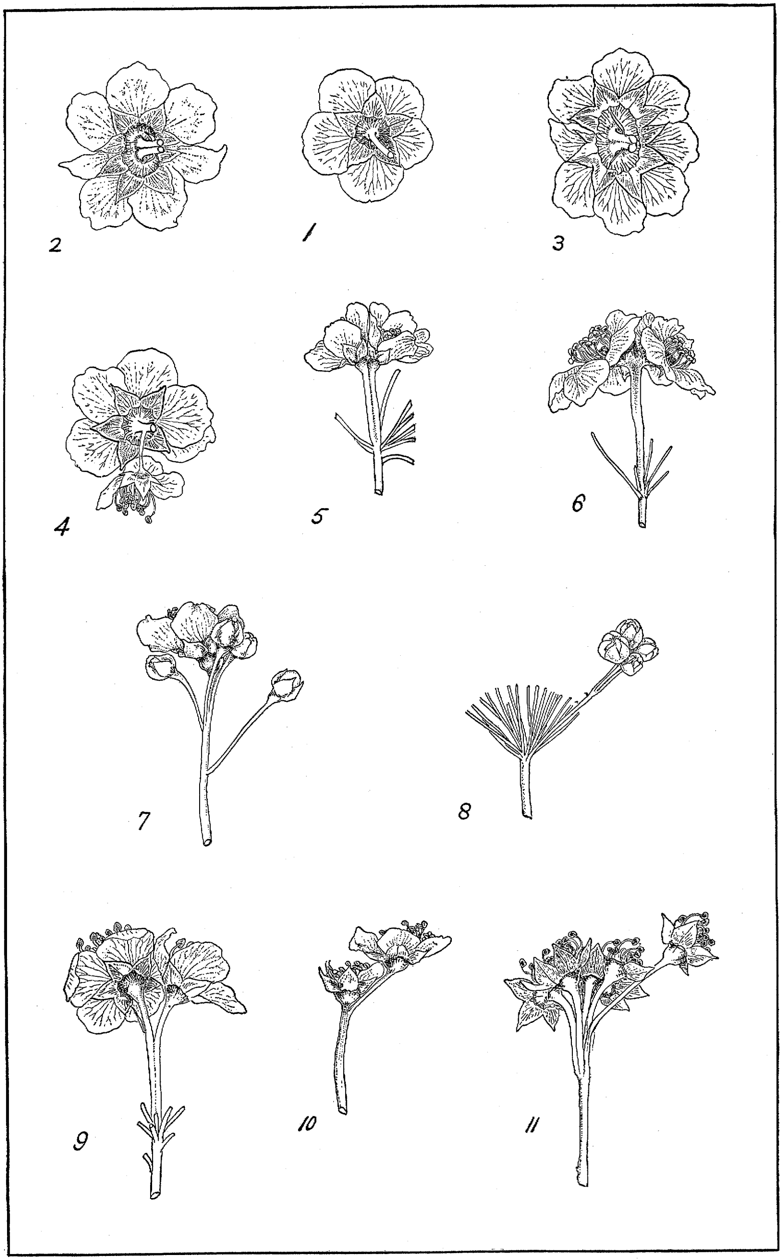

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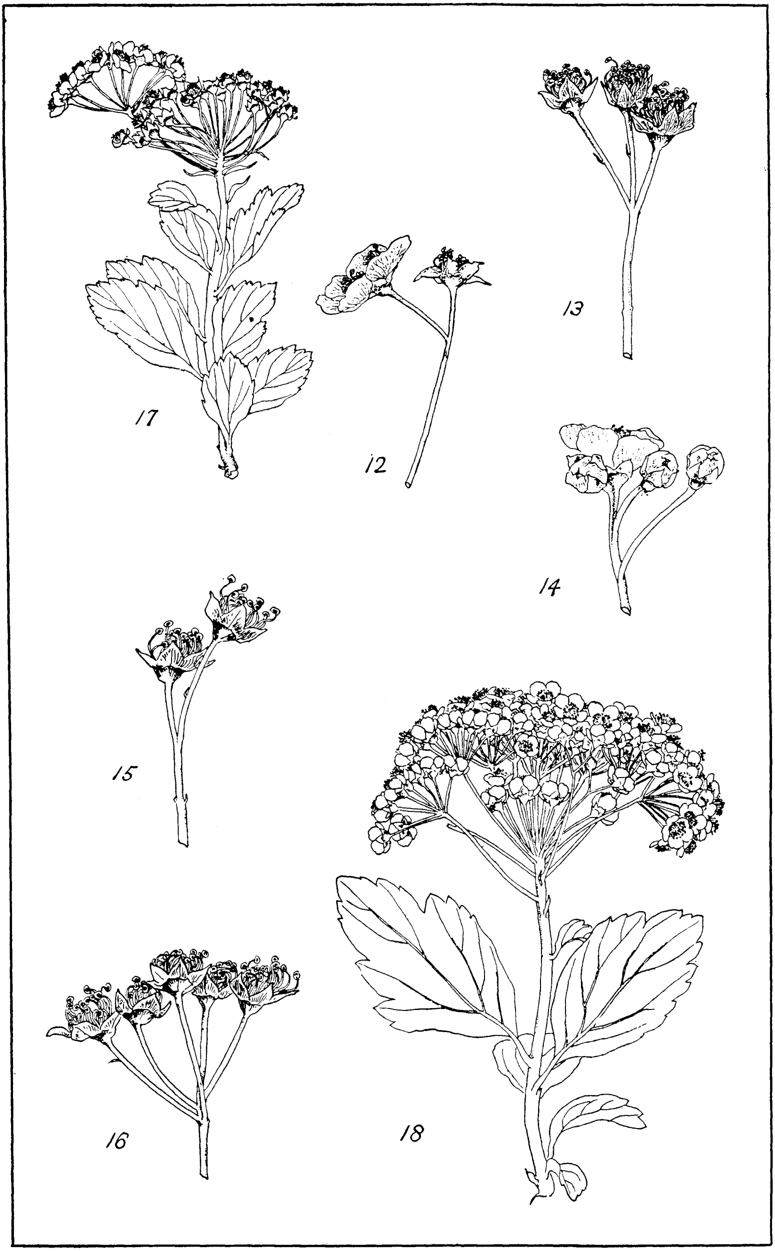

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